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A MODEL DESCRIPTIVE OF GREGARIOUSNESS OF COLONIAL INSECT LARVAE

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INTRODUCTION

Aggregation in insects, as with other animals, appears to be a fundamental trait with complex origins. Needless to say, it has a direct bearing on reproduction and survival, both of which are vital factors in the population dynamics.

Many ecologists and mathematicians have been interested in the aggregation of animals or plants, and have proposed statistical models to describe the spatial pattern of the distributions, or measures of aggregation to test departures of the distributions from randomness (see Southwood 1978). However, only a few studies have considered the ecological and behavioural sapects of aggregation (Morisita 1952, Breder 1954, Shigesada and Teramoto 1978).

Many factors are supposed to be operating on the

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aggregation of insects. Morisita (1961) classified ecological factors that form aggregations into three categories: (1) response to environmental heterogenity, (2) mutual attraction with other individuals of the same species (e.g.,gregariousness or mating behaviour), and (3) reproductive behaviour (e.g., issuance from egg-masses or clumped eggs with limited movement of subsequent stages). The effective or dominant factors that form aggregation will change from species to species. Each student directed his attention, according to his investigating objects, to one of these factors. For example, Morisita (1952), who studied habitat selection of ant-lion, directed his attention to the response to the environmental heterogenity, and Breder (1954), who studied schooling of fish, to the mutual attraction of individuals.

Most colonial insects as we know lay eggs in clusters and the larvae emerged from each cluster tend to be gregarious and to stay within a certain range from the cluster. Therefore, we should take into consideration both the mutual attraction of individuals and the reproductive behavioural performance for the study of gregariousness of colonial insects. In this paper, we will propose a simple model incorporating both these factors to describe the distribution of individuals, and show a new method analyzing the aggregation pattern of colonial insects. We will also describe the application of

the method to data obtained on the larval distribution of a colonial insect Pryeria sinica Moore.

MODEL

Generally, colonial insects lay eggs in cluster and ensuing larvae distribute themselves in discrete habitat units such as trees, shoots or leaves. These habitat units are usually used as the sampling units and provide natural bases of defining spatial distribution patterns. Let us assume, for simplicity, that these habitat units are arranged in one-dimensional space (Fig.1). The units are possible to be numbered,from left to right, one to infinitive. An egg cluster is assumed to be oviposited near the first unit where the initial aggregation of hatchlings is made. The clump size (total number of individuals that included in the aggregation) is expressed as N. Each individual is considered as both repulsive and attractive to some extent. In this model, individuals tend to disperse to the right from the first unit and return to the left units to aggregate.

If the number of individuals in the i-th unit at time t is indicated by $n_i(t)$, the number of individuals moving from the i-th unit to the $(i+1)$-th unit within a unit time is represented by $D_{i,i+1} \cdot n_i(t)$ and those from the i-th unit to the $(i-1)$-th unit by $D_{i,i-1} \cdot n_i(t)$, where $D_{i,i+1}$ and $D_{i,i-1}$

indicate probabilities of movement of an individual in the $\underline{i}$-th unit to the right adjacent unit and to the left adjacent unit, respectively. The assumption has a restriction that the individual moves in unit steps; at each step the individual does not have probabilities to move from the i-th unit to the (i±m)-th unit ($m \geq 2$).

Then, the rate of change in the number of individuals in each unit is represented as the folloing differential equation:

$$\frac{dn_1}{dt} = - D_{1,2} \cdot n_1(t) + D_{2,1} \cdot n_2(t)$$

$$\frac{dn_2}{dt} = D_{1,2} \cdot n_1(t) - D_{2,1} \cdot n_2(t) - D_{2,3} \cdot n_2(t) + D_{3,2} \cdot n_3(t)$$

$$\vdots$$

$$\frac{dn_i}{dt} = D_{i-1,i} \cdot n_{i-1}(t) - D_{i,i-1} \cdot n_i(t) - D_{i,i+1} \cdot n_i(t) + D_{i+1,i} \cdot n_{i+1}(t)$$

$$\vdots \qquad (1)$$

Considering that each unit has carrying capacity $\underline{K}$, we assume

$$\underline{D}_{\underline{i},\underline{i+1}} = \alpha_1 \left(1 - \frac{\underline{n}_{\underline{i+1}}(\underline{t})}{\underline{K}} \right) \qquad \text{for } \underline{n}_{\underline{i+1}} < \underline{K}$$

$$= 0 \qquad \text{for } \underline{n}_{\underline{i+1}} \geq \underline{K}$$

and

$$\underline{D}_{\underline{i+1},\underline{i}} = \alpha_2 \left(1 - \frac{\underline{n}_{\underline{i}}(\underline{t})}{\underline{K}} \right) \qquad \text{for } \underline{n}_{\underline{i}} < \underline{K}$$

$$= 0 \qquad \text{for } \underline{n}_{\underline{i}} \geq \underline{K}. \quad (2)$$

From these assumptions, a unit occupied by more individuals than $\underline{K}$ cannot be entered from the adjacent units and a probability of entrance into a unit occupied by fewer individuals than $\underline{K}$ is proportional to a ratio of the vacant posts to the carrying capacity. The constants α_1 and α_2 represent strength of dispersal and aggregation, respectively.

If the number of individuals in the $\underline{i}$-th unit, $\underline{n}_{\underline{i}}(\underline{t})$ follws equations (1) and (2), and if $\alpha_1 < \alpha_2$, $\underline{n}_{\underline{i}}(\underline{t})$ approaches to an equilibrium value $\underline{n}_{\underline{i}}$ which satisfies the next equation:

$$\alpha_1 \cdot \left(1 - \frac{\underline{n}_{\underline{i+1}}}{\underline{K}} \right) \cdot \underline{n}_{\underline{i}} = \alpha_2 \cdot \left(1 - \frac{\underline{n}_{\underline{i}}}{\underline{K}} \right) \cdot \underline{n}_{\underline{i+1}} \qquad (3)$$

that is, individuals moving within a unit time from the i-th unit to the $(i+1)$-th unit is equal in number to those moving from the $(i+1)$-th unit to the i-th unit at equilibrium. If $\alpha_1 \geq \alpha_2$, then all the individuals disperse infinitely and no equilibrium can be attained.

We put

$$\alpha = \frac{\alpha_2}{\alpha_1} \tag{4}$$

The parameter α represents gregarious intensity, i.e. a measure of intensity of aggregation against dispersal.

By solving equation (3), each n_i is expressed by the number of individuals being in the first unit n_1:

$$n_i = \frac{K}{1 + \alpha^{i-1} \cdot \left(\frac{K}{n_1} - 1 \right)} \tag{5}$$

The value n_1 is determined via relation,

$$\sum_{i=1}^{\infty} n_i = N \tag{6}$$

if values of α, K and N are given.

Unfortunately, however, we cannot explicitly solve the equation for $\underline{n}_1$, and so we use an integral approximation as shown in Fig. 2. The value $\underline{n}_{\underline{i}}$ is expressed as an area of a square between $\underline{x}=\underline{i}-1$ and $\underline{x}=\underline{i}$, and a continuous curve $\rho(\underline{x})$ is drawn such as $\rho(\underline{i}-\frac{1}{2})=\underline{n}_{\underline{i}}$. Inquiring equation (5)[1], we can give a form

$$\rho(\underline{x}) = \frac{\underline{K}}{1 + \underline{A}\,\alpha^{\underline{x}}}, \tag{7}$$

The constant $\underline{A}$ is determined by the following approximation,

$$\int_0^{\infty} \rho(\underline{x})\,\underline{dx} \simeq \underline{N}. \tag{8}$$

We can now integrate (8), getting

$$\underline{A} = \frac{1}{\alpha^{(\frac{\underline{N}}{\underline{K}})} - 1}. \tag{9}$$

The number of individuals at equilibrium may be approximated

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[1] We put $\underline{i}-\frac{1}{2} = \underline{x}$ and $\alpha^{\frac{1}{2}} \cdot (\frac{\underline{K}}{\underline{n}_1} - 1) = \underline{A}$ in the right hand side in equation (5).

by

$$\underline{n}_{\underline{i}} \simeq \int_{\underline{i}-1}^{\underline{i}} \rho(\underline{x})\,d\underline{x} = \frac{\underline{K}}{\ln \alpha} \ln\{ \frac{\underline{A} + \alpha^{-\underline{i}+1}}{\underline{A} + \alpha^{-\underline{i}}} \}. \qquad (10)$$

By computer calculations the above approximation (10) was confirmed to correspond closely with the original equations (5) and (6) (the error is less than 0.1% for $\underline{K}>0$, $\underline{N}>0$ and $\alpha>1$). The equilibrium distributions of individuals among units are drawn in Figs. 3 and 4 for different values of α (represented as $\ln \alpha$ in Fig. 3) and $\underline{N}$, respectively. We can see that the number of individuals in the left units come close to carrying capacity $\underline{K}$ as $\underline{N}$ increases and that the pattern of distribution shows more intense aggregation for larger values of α.

If we get a set of observed values of $\underline{n}_{\underline{i}}$ in a clump of size $\underline{N}$, we can determine the specific parameters α and $\underline{K}$ for the clump by the method of least squares. However, to obtain the representative estimates of those parameters for a given population, it is desiable to obtain the estimates from data on several different sized clumps sampled from the population.

For this purpose, we applied a parameter mean concentration, proposed by Iwao (1976), to our model. Mean concentration is defined as the mean number of individuals per individual

per quadrat,i.e.,

$$\underline{c}^* = \frac{\sum_{\underline{j}=1}^{\underline{q}} \underline{n}_{\underline{j}}^2}{\sum_{\underline{j}=1}^{\underline{q}} \underline{n}_{\underline{j}}} \tag{11}$$

where $\underline{n}_{\underline{j}}$ is the number of individuals in the $\underline{j}$-th quadrat, $\underline{q}$ is the total number of quadrats contained in the population area. We replaced his quadrat by our habitat unit, and then,

$$\underline{c}^* = \frac{\sum_{\underline{i}=1}^{\infty} \underline{n}_{\underline{i}}^2}{\sum_{\underline{i}=1}^{\infty} \underline{n}_{\underline{i}}} = \frac{1}{\underline{N}} \sum_{\underline{i}=1}^{\infty} \underline{n}_{\underline{i}}^2. \tag{12}$$

Substituting equation (9) and (10) to (12), $\underline{c}^*$ is represented as a function of α, $\underline{K}$ and $\underline{N}$:

$$\underline{c}^* = \frac{1}{\underline{N}} \sum_{\underline{i}=1}^{\infty} \left\{ \frac{\underline{K}}{\ln \alpha} \ln \frac{1+(\alpha^{(\frac{\underline{N}}{\underline{K}})} - 1)\ \alpha^{-\underline{i}+1}}{1+(\alpha^{(\frac{\underline{N}}{\underline{K}})} - 1)\ \alpha^{-\underline{i}}} \right\}^2. \tag{13}$$

The value of $\underline{c}^*$ illustrated in Fig. 5 was numerically calculated for different values of α (represented as ln α in the figure). We can see that each curve on the graph has a linear part near the origin and that $\underline{c}^*$ approaches an asymptote $\underline{K}$ as $\underline{N}$ increases. For small values of α, the curves are monotonously increasing but, for large values, they show wave-like oscillation. The gradient of the linear part near the origin can be obtained as follows.

As $\underline{N}$ is much smaller than $\underline{K}$ near the origin, we can neglect $\underline{n}_{\underline{i}}/\underline{K}$ and $\underline{n}_{\underline{i}+1}/\underline{K}$ in equation (3) and get,

$$\underline{n}_{\underline{i}} \simeq \alpha \cdot \underline{n}_{\underline{i}+1}. \tag{14}$$

We can determine $\underline{n}_{\underline{i}}$ as a function of $\underline{N}$ and α as

$$\underline{n}_{\underline{i}} \simeq \underline{N} \cdot (\alpha - 1) \cdot \alpha^{-\underline{i}}. \tag{15}$$

Substituting equation (15) to (12), $\underline{c}^*$ can be represented as

$$\underline{c}^* \simeq \frac{\alpha - 1}{\alpha + 1} \underline{N}. \tag{16}$$

Therefore, the gradient near the origin is $\dfrac{\alpha - 1}{\alpha + 1}$.

If observational or experimental data of distributions are obtained for clumps of different sizes, we can plot $\underline{c}^*$ calculated from equation (13) versus $\underline{N}$, roughly estimating

the parameter of gregarious intensity α from the gradient of the curve and the carrying capacity $\underline{K}$ from the asymptote. The more detail value of α and $\underline{K}$ can be obtained by the method of least squares (computer will be indispensable).

As this method need laborous calculation of equation (13), the following procedures will be convenient. For small value of α, the next equation is approximately satisfied:

$$\sum_{\underline{i}=1}^{\infty} \underline{n_i}^2 = \int_0^{\infty} \{\rho(\underline{x})\}^2 \underline{dx} \tag{17}$$

As the result, we get

$$\underline{c}^* = \underline{K}\left\{1 - \frac{\underline{K}}{\underline{N} \cdot \ln \alpha}\left(1 - \alpha^{-(\frac{\underline{N}}{\underline{K}})}\right)\right\}. \tag{18}$$

We can use the above simple equation in place of equation (13) for small α. Computer calculation shows that maximum of errors of $\underline{c}^*$ in equation (18) is 1% for α=3.0 and 10% for α=6.0. Therefore, whenever the value α obtained by the use of equation (18) is less than 6.0, we can estimate the value within 10% errors.

When the obtained value α is larger, we adopt only $\underline{K}$ value but α because $\underline{K}$ is little influenced by the approximation of equation (17). Then we transfer c* and N obtained from the data to c*' and N' as follows,

$$\underline{c}^{*\prime} = \underline{c}^{*} \frac{100}{\underline{K}}$$

$$\underline{N}' = \underline{N} \frac{100}{\underline{K}} \qquad (19)$$

taking the best fitting curve among the graphs with different α and constant $\underline{K}$=100 as shown in Fig. 5.

APPLICATION OF THE MODEL

Material and acquisition of the data

The applicability of our method is now examined on Pryeria sinica (Zyganidae:Lepidoptera). We will briefly describe here the bionomics of this species. P. sinica has a univoltine life cycle in Fukuoka. Adult emerges at the beginning of November. A female oviposits her eggs in a cluster near a wintering bud of the host plant, Euonymus japonicus. The number of eggs in a cluster ranges from 60 to 180. It overwinters as egg stage and the eggs usually hatch at the end of February. The hatchlings feed young leaves of the host plant in a clump but they separate themselves into several sub-clumps as they become larger. The larvae of a single clump show a synchronized development. Fully grown larvae can be seen at the end of May.

Investigations were made at a hedge-row of E. japonicus in the Experimental Field of the Department of Biology, Kyushu University from March to April, 1979. When we found a clump of larvae at the hedge, it is first examined whether the clump is issuance from a mass of eggs or not. The examination can be easily made by counting the number of masses of egg-shells remained near the larval clump on the hedge. When the clump was found to be issuance from a mass of eggs, the number of individuals were counted on each habitat unit (young shoot of E. japonicus) in which the larvae occurred. On the other hand, when the clump was found to be issuance from two or more egg masses oviposited separately, no counting was made, as complicated disturbing factors were supposed to be operating on the distribution pattern of individuals. The investigations were made on each instar of larvae from the first to the fourth (final) instar. As clump size is usually large at younger larval stages, we settled artificially small clumps of larvae on shoots to obtain additional data. The investigations on these clumps were made two or three days after the artificial settlings.

Results

The results of investigations were summarized in Fig. 6 (a-d). The results on the artificially settled clumps are represented by hollow circles in the figure. The curve-linear

regression for the observed relation is obtained from the equation (13) by computer calculation using the method of least squares.

The estimate of α (gregarious intensity) and $\underline{K}$ (carrying capacity) for the first instar larvae are 12.77 and 185.1 respectively (Fig. 6(a)). The strength of aggregation is 12.77 times greater than that of dispersal. Values of the parameter α for the second, the third and the fourth instar larvae are estimated as 6.00, 2.60 and 1.78, respectively, decreasing according to the development of the larval instar (Fig. 7). Values of the parameter $\underline{K}$ for the second, the third and the fourth instar larvae are estimated as 77.0, 28.1 and 2.73, respectively. The carrying capacity of the habitat unit also decreases with the larval development (Fig. 7).

The estimations of parameters from equation (18) are also made. The results are shown in Table 1 together with the estimates from equation (13). We can see that $\underline{K}$ value does not so differ with two different methods in each larval instar. However, α value estimated on the first instar larvae by equation (13) is largely different from that estimated by equation (18), because the approximation by equation (17)

is not good for large value of α. In this case, we should not adopt α value estimated from equation (18) but adopt that from equation (13).

DISCUSSION

There have been proposed many indices of aggregation based on quadrat counts. Among them, variance-to-mean ratio, negative binomial parameter k, Iδ-index proposed by Morisita (1959) and mean crowding by Lloyd (1967) are widely used as good measures of aggregation. As stated by many authurs, each measure of aggregation is dependent in part on the size of sampling unit chosen. Morisita (1959) and Iwao (1972) applied this nature of indices (Iδ-index and mean crowding respectively) to detect spatial pattern of individuals within a clump and distinguished different pattern of distribution of random, aggregated and uniform. These methods are useful to find clumps where the individuals are scattered throughout a continuous space.

On the other hand, investigating the aggregation patter of colonial insects in their natural field, we are usually faced by a situation that the individuals occur in discrete habitat which surve as natural sampling unit. Clump size of colonial insects is often able to be measured directly even when members of the clump may separate themselves into

several sub-clumps. Considering these characteristics of colonial insects, we proposed a model to analyse spatial structure of a clump with a new parameter of aggregation, α.

It is usually taken for granted that the clump size is highly variable among clumps. Though this high degree of variability often makes the estimation of measure of the aggregation so imprecise, no study seems to have been made on the variability of the clump size. As shown in Figs. 5 and 6, $\underline{c}^*$ has curve-linear relationship to the clump size $\underline{N}$. Single estimate of α for a clump indicates only a specific value of that clump. We should know species specific α from the relationship between $\underline{N}$ and $\underline{c}^*$ for the study of gregariousness of an insect species. If equation (13) represents the true nature of aggregation, we can see it by measuring aggregations on three or more clumps with different clump size.

We considered that the distribution of individuals is partly determined by a balance between dispersing and aggregating strength which are expressed as α_1 and α_2 in our model. Similar idea can be seen in Breder (1954) and Kennedy and Crawley (1967).

Breder measured distance between nearest neighbours, explaining the exsisting mechanism of schooling of fish by a balance between repulsion and attraction of the individuals.

Kennedy and Crawley (l.c.) analyzed distribution of aphids, Drepanosiphum platanoides on a sycamore leaf in the similar way, and found that they repel one another up to a certain distance despite that they exhibit gregarious behaviour. They termed such a behaviour spaced-out gregariousness, suggesting that it would be fruitful to consider every insects are solitary and gregarious at the same time, i.e. both repelling and attracting conspecifics. We applied this idea to our method that use discrete habitat units in spite of the distance measurements. In this case, there exist a maximum number of individuals that enter a habitat unit. In this sense, our model belongs to one of density dependent models, in which case the movement depends on the density of the entered unit.

Kennedy and Crawley (l.c.) used both terms attracting and repelling in loose sense referring only to changes in spacing, without necessarily implying directed movement. In our model, we assumed the directional movement of individuals from a center which will be taken place by the reproductive behaviour of colonial insects. The directional movements are seen other than colonial insects. For example, Morisita (1950) studied density related movements

of adult Gerris lacstris (Hemiptera:Gerridae) among several adjacent small ponds in the study area. Adult density became higher in one of those ponds than the others in the early periods of the adult immigration from hibernating sites. As it seemed to reach a saturation density, a fraction of individuals on that pond became to emigrate onto other ponds. The rate of emmigration increased with the density of that pond. These adult movements determined the distribution of individuals among the ponds. Similar density dependent movements are found in many insects, e.g., ahids Aphis glycines, Rhopalosiphum maidis, R. padi and Macrosiphum granarium (Ito 1952,1960), sugar cane bug Cavelelerium saccharivorus (Murai 1977), several species of dragon flies of Anisoptera (Moore 1964, Higashi 1969) and Zygoptera (Moore 1964).

Morimoto (1972) reviewed the studies on the insect aggregations. He stated that the group size of larvae differs among different species or differnt larval stages of the same species. As already made clear, however, the group size (number of individuals in a habitat unit in our model) is influenced not only by the intensity of aggregation of the insect but also by both the clump size and the carrying capacity of the habitat unit. These components will be required to be distinguished. In our model, they are represented separately by the parameters α, N and K, respectively. Using these parameters,

we will be able to make a comparative study among different species of colonial insects.

SUMMARY

A model is constructed to describe gregariousness of colonial insect larvae which occur in discrete natural habitat units. The model is based on the assumption that the distribution of individuals in a clump is determined by a balance between aggregative and dispersing movements of individuals. The model includes three parameters, i.e., clump size, carrying capacity of habitat units and intensity of aggregation against dispersal. The modes of effects of these parameters on the distribution of individuals are analyzed.

Several methods are developed to estimate these parameters from observed data, and their applicabilities are investigated. Application of these methods are described on the larval distribution of a colonial insect Pryeria sinica Moore.

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Table 1. Values of parameters α and K estimated from equation (13) and (17).

	Estimate from equation (13)		Estimate from equation (17)	
	α	K	α	K
1st instar larva	12.77	185.1	7.69	198.4
2nd "	6.00	77.0	5.32	77.3
3rd "	2.60	28.1	2.53	28.2
4th "	1.78	2.73	1.79	2.71